The Bone-Eating Dog, *Borophagus diversidens* Cope

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The first-named species of the late Tertiary bone-eating or hyaenoid dogs (*Borophagus, Osteoborus*) is *Borophagus diversidens* Cope, based on a specimen from the Blanco formation of Texas. The species has, until now, been known from only a few fragmentary specimens.

In the past several years field parties from Midwestern University have made extensive collections in the Blanco formation. During part of this time Mr. and Mrs. John Carter, of Wichita Falls, Texas, have also collected there. The Carter collection has recently been acquired by Midwestern University, and among the specimens included are the skull, lower jaw and some postcrannial elements of a specimen of *Borophagus diversidens*. These, combined with the more limited material in the university collection, permit more adequate description of the species than was hitherto possible.

History of Species

The description of *Borophagus diversidens* has been the source of much confusion, and attempts of later authors to clarify it have, in some instances, only compounded it. Some errors have persisted in the literature to the present time. Papers pertinent to understanding the problem are summarized here.

Edward D. Cope, on October 11, 1892, made an oral report to the members of the Academy of Natural Sciences of Philadelphia, regarding carnivore fossils found the previous year in the Blanco beds of Texas. A brief summary was published in the Proceedings of the Academy (Cope, 1892a). Three species were discussed, *Borophagus diversides, Felis hillianus,* and *Canimartes cumminsii.* The latter two are only mentioned, and as used at that time the names are *nomina nuda.* For *Borophagus,* however, supposedly

diagnostic characters are given, a lower jaw is described with detailed measurements of teeth, and a definite type locality is cited. The paper constitutes a valid description of the genus and species.

Under the identical title, "A Hyaena and Other Carnivora from Texas," an account appeared in the American Naturalist, December, 1892 (Cope, 1892b). This begins "At a meeting of the Philadelphia Academy," and then follows an exact copy of the summary in the Proceedings of the Academy of Natural Sciences of Philadelphia. I am unable to determine which paper has priority but presumably that of the Philadelphia Academy appeared earlier and the name should date from it.

The following year a detailed account of the fauna of the Blanco beds was given (Cope, 1893). The holotype jaw of *Borophagus diversidens* was figured and the names *Felis hillianus* and *Canimartes cumminsii* were validated. In the account of *Borophagus*, Cope cited the paper in the American Naturalist as the original description.

Cope here discussed a second specimen which he thought pertained to *Borophagus diversidens*. "Another specimen included the separate crowns of three molars, including part of the sectorial." It is this second, referred, specimen that has caused most of the confusion and controversy surrounding *Borophagus diversidens*. Both the holotype jaw and referred specimen were originally in the collection of the University of Texas but in 1893 Cope reported that the referred specimen had been lost.

Merriam (1903) described *Hyaenognathus pachyodon* from California. He noted the close resemblance of the lower premolars of *Borophagus* to those of his new form, but found the lower molar of his specimen different from that of Cope's referred specimen. Martin (1928) described a small species of canid from Kansas as *Hyaenognathus cyonoides*. Matthew and Stirton (1930) placed *cyonoides* in the genus *Borophagus* and referred to *Borophagus cyonoides* the skulls, jaws, and postcranial material from Hemphill County, Texas. Matthew and Stirton also reviewed the status of *Borophagus diversidens and Hyaenognathus pachyodon*, comparing both with *B. cyonoides* but not with each other. They noted that the holotype of *Borophagus diversidens* was then lost.

Stirton and VanderHoof (1933) reappraised the status of the then known bone-eating dogs. They made *Hyaenognathus cyo-*

noides the type of a new genus, *Osteoborus.* They critically reviewed Cope's description of *Borophagus,* noted the similarity of the holotype to Merriam's *Hyaenognathus pachyodon,* but did not unite *Hyaenognathus* with *Borophagus* because the holotype of the latter was lost. They thought Cope's referred specimen belonged to a genus other than *Borophagus.*

Shortly thereafter VanderHoof (1936) reported that Stirton had searched the collection at the University of Texas and rediscovered the holotype and referred specimen of *Borophagus diversidens.* The holotype was figured, measurements given, and *Hyaenognathus* was formally declared a synonym of *Borophagus.*

VanderHoof also stated that Cope's referred specimen consisted of "milk teeth of a large dog close to *Canis dirus,* and a worn M^1 of the same." This is almost certainly wrong. Cope stated that the referred specimen consisted of teeth from a single jaw. He would scarcely have confused milk teeth and worn permanent upper teeth. Recognition of the original teeth would be virtually impossible, for they were never figured or referred to by a catalogue number. VanderHoof was under the impression that the 1893 description was the original description, and referred to the "paratype" teeth. This error has been followed by some later workers. There was no paratype. Only one specimen, the holotype, was mentioned in the original description, whichever of the 1892 papers has priority.

Felis hillianus Cope (1893) was based on a canine tooth, part of a vertebra, and foot bones from the Blanco formation. Matthew and Stirton (1930) showed that the foot bones belonged to a canid, and referred them to *Borophagus diversidens.* VanderHoof (1937) stated that the *Felis hillianus* material probably belonged to *Osteoborus,* not *Borophagus.* His conclusions are demonstrably wrong, for foot bones recently taken in close association with the *Borophagus* skull match the specimens figured by Cope. *Felis hillianus* is a synonym of *Borophagus diversidens.*

It should be emphasized that *Borophagus diversidens* is based on a single specimen, a holotype. Cope's referred specimen was lost more than 70 years ago, and there is no good reason to consider it further. What it is or is not has absolutely no taxonomic importance as far as the name *Borophagus diversidens* is concerned.

Meade (1945) reported on the extensive collections made in the Blanco formation during 1941-43, and largely catalogued at the

University of Texas.   He recorded an upper jaw fragment and calcaneum of *Borophagus*, the first specimens found in the Blanco deposits in more than 50 years.   Meade noted that, in attempting to place Cope's troublesome "paratype" and *Felis hillianus* in the synonomy of species other than *Borophagus*, VanderHoof had included both *Canis dirus* and *Osteoborus* as members of the Blanco fauna.   Meade found no specimens from the Blanco formation referable to either.   The same may be said for the present collection. As Meade pointed out, the presence of some species of *Canis* in the Blanco would not be surprising, but none has been taken there. *Canis dirus*, so far as I am aware, is known only from late to moderately late Pleistocene deposits.   Its presence in the Blanco is unlikely.   The presence of *Osteoborus*, the probable direct ancestor of *Borophagus*, in the Blanco, is also unlikely.

Hibbard and Riggs (1949) described the right maxillary and two upper left molars of a *Borophagus* from the Rexroad formation of Kansas.   Dr. Hibbard (personal communication) has informed me that he has since concluded that this specimen is not *B. diversidens*.

Hibbard (1950) figured a fragmentary lower jaw of *B. diversidens* found 7 miles northeast of Crosbyton, Texas, by J. LeRoy Kay, and now in the Carnegie Museum.   This specimen may have come from the Blanco formation.   I know of no other records or specimens of *B. diversidens*.

DESCRIPTION

The new material representing *Borophagus diversidens* includes the following parts of the skeleton of one individual (MU8034): the skull, right mandible, axis, 7th cervical vertebra, 2 caudal vertebrae, parts of several other vertebrae, several rib fragments, right humerous, left ulna lacking olecranon, right radius and proximal end of left, much of the pelvis, left femur lacking distal end, head of right femur, left tibia, much of left fibula, and a number of foot elements.   Available also are isolated bones as follows: a right mandible, lacking ascending ramus but with canine and alveoli or roots of remaining teeth, an isolated canine, two broken lower carnassials, a complete radius, and an ulna without the distal end.

The skeleton belonged to a young adult dog with teeth only lightly worn.   The skull is nearly complete, lacking only the posterior part of the lambdoidal crest, a bit of the interorbital region,

small fragments of both zygomatic arches, and some minor details. There is some distortion. The thin laminar surface of the bones of the dorsal surface of the skull are greatly shattered. In addition, the bone of the supraorbital area and the left nasal have been driven in and broken free. This appears not to be post-mortem damage, and may represent the fatal blow from the hoof of some ungulate. The ventral surface of the skull is fairly well-preserved, but the palate is severely cracked. The skull was found in two parts, the cranium with most of the zygomatic arches attached and the separated rostrum. A bit of the interorbital region was missing, and there was no point of contact between the two skull fragments. The missing interorbital region has been restored with plaster, by using the lower jaw to determine approximately correct proportions.

The dentition, both upper and lower, is excellent. In the skull, the right first incisor is broken off at the root and the left first premolar is missing. Otherwise all teeth are present. In the lower jaw, two incisors are lost, and the second premolar is gone, though the alveolus is well-preserved.

Upper Dentition

Upper incisors 1 and 2 are small and crowded. The third incisor is much larger and stouter. The canine is heavy and subcircular at the base. The first, second, and third premolars are approximately oval in shape, low, and have almost flat surfaces. The first is distinctly smaller than the second; the second scarcely smaller than the third. The teeth vary somewhat in size, shape, and placement in the tooth row on the two sides of the skull. Hibbard and Riggs (op. cit., p. 838) found no evidence of an upper P^1 in the maxillary fragment from Kansas. The P^1 is present on both sides of the skull from the Blanco.

The carnassial, P^4, is a huge tooth. There is no parastyle, and the tooth agrees with the generic characters as set forth by Vander-Hoof and Gregory (1940). On the anterior face of the tooth, in the position the parastyle would occupy, a slight bulge can be felt, and a barely detectable swelling noted.

M^1 is large and broad. M^2 is relatively large for a posterior molar. It is placed lingual to the outer border of M^1, and in lateral view is largely concealed behind the first molar.

Fig. 1. Skull of *Borophagus diversidens,* lateral and ventral view. The teeth have been outlined in the ventral view.

LOWER DENTITION

The lower jaw is nearly complete, except that a few small fragments of the ascending ramus are lost. The upper part of the ascending ramus is somewhat broken but there appears to be no distortion.
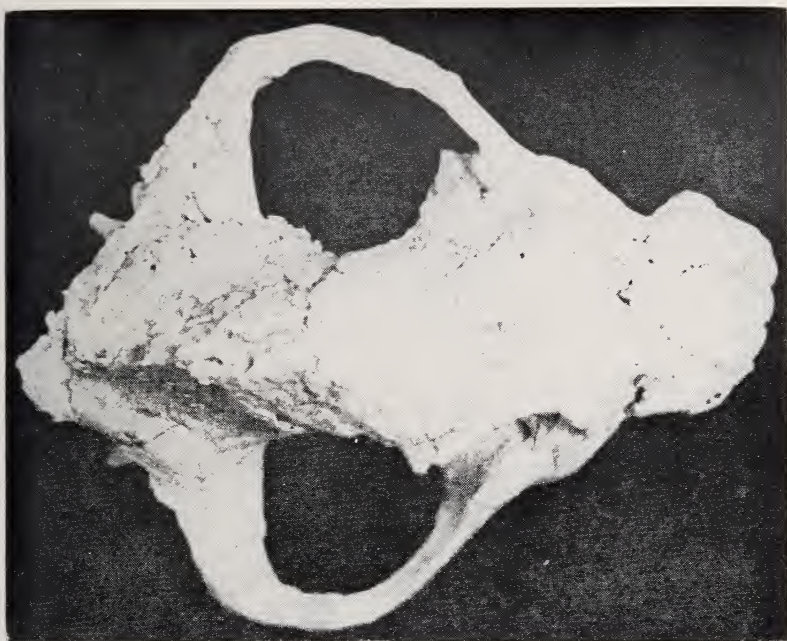
Fig. 2. Skull of *Borophagus diversidens,* dorsal view.

The two inner incisors are lost and most of the alveoli for them has been broken away. The teeth were obviously small. I_3 is a rather large incisor and is separated from the canine by a slight gap. The canine is stout and thick for a canid. There is no P_1. P_2 is missing but the alveolus shows this to be a distinctly smaller tooth than P_3. P_3 is oval and flat-crowned, like the anterior upper premolars. It is single-rooted. P_4 is a huge, posteriorly-inclined conical structure. Its posterior surface is curved to conform to the anterior face of the carnassial. There is a single weak cusp on the posterior surface, rather than two distinct "stepped" cusps as are found in *Osteoborus* and other bone-eating dogs.

The carnassial, M_1, is an enormous, elongated tooth. It departs from the generic characterization as set forth by VanderHoof and Gregory (op. cit., p. 144) in having a small but distinct metaconid. Two other lower carnassials available also have the metaconid present and developed to the same degree. Seemingly the presence of the small metaconid is a specific character separating *B. diversidens* from *B. pachyodon.*

Fig. 3.   Lower jaw of *Borophagus diversidens* in lateral and dorsal view. Bases of teeth have been outlined.

M_2 is a small, oval, flat-crowned tooth. M_3 is a smaller, rounded flat-crowned tooth.

The cranial measurements in the appendix are only approximate because the surface of the bones of the skull are crushed and distorted.   They do give an idea of the general size and shape of the specimen.   The measurements of the tooth rows are more accurate, but some slight errors resulting from cracking and distortion may be present.   The bone of the lower jaw is firm and undistorted. Measurements in the appendix are accurate.

Measurements of individual teeth were made as though the teeth were separate from the jaw.   The first measurement is the greatest diameter of the tooth in a general anteroposterior axis, regardless of its actual orientation in the tooth row.   The second

measurement is the greatest transverse diameter, taken at right angles to the length. This method of measurement seems to be the most meaningful. In the skull, the same teeth on the two sides of the jaw are usually similar in size and shape, but are often set differently in the tooth row. Anteroposterior measurements, taken parallel to the long axis of the skull, result in deceptively different figures. This is especially true of the anterior premolars, and it is clear that even greater variations would be evident if different skulls or jaws were compared.

Postcranial Skeleton

The postcranial skeleton of *Borophagus diversidens* is peculiar in several respects, and the living animal must have been unusual in appearance. The head was larger than that of a modern gray wolf, and much broader and higher. The neck was stout and strong, to support the heavy head. The body, however, was relatively small. The upper limbs were as long as those of the gray wolf, but the lower limbs were much shorter. Both upper and lower limbs were much stouter than those of the wolf. Since the metapodials were scarcely more than half as long as those of the modern wolf, the feet must have been very short and stubby. *Borophagus* was clearly not a swift-footed animal, and its gait is difficult to visualize.

The axis, compared with that of the gray wolf (*Canis lupus*) has a stouter, heavier neural arch and neural spine. The centrum is broader but shorter. The odontoid process is relatively short and thick. As compared with the axis of *Osteoborus cyonoides,* from the middle Pliocene (type Hemphillian) Coffee Ranch local fauna, of Hemphill County, Texas, the axis of *Borophagus* is larger and has a narrower neural spine but is otherwise quite similar. The odontoid process is equally short and stout.

The 7th cervical vertebra has the centrum as long as that of the gray wolf but is wider and deeper. The zygapophyses are broader and stronger. The neural spine is longer, and the neural arch beneath the spine is thicker. The neural canal is relatively broader and lower, more oval, in shape. Compared with *Osteoborus,* the vertebra is very similar in shape but larger. The neural arch, at the base of the neural spine, is more hollowed out posteriorly.

The humerus is as long as that of the gray wolf but is stouter and more curved. The space between the internal and external tuberosities is less deeply grooved. The shaft is thicker. The distal end is much wider. The ulnar fossa is wider and the lateral condyles much broader. There is no trace of an entepicondylar foramen, and the structure of the humerus is so thick and rounded at this point that one could scarcely exist. The humerus of *Borophagus* is larger but generally similar in shape to that of *Osteoborus* but has a stronger ridge on the front of the shaft. The distal end is relatively broad, as in *Osteoborus*, but differs from the humerus of *Osteoborus* in the absence of the entepicondylar foramen. In eight of nine available *Osteoborus* humeri, the foramen is present and developed to about the same degree. In one specimen there is a notch in the side of the humerus, where the outer wall of the foramen failed to ossify.

Fig. 4. Limb bones of *Borophagus diversidens* compared with those of a young-adult gray wolf, *Canis lupus*. Left to right: humeri, radia, femurs, tibias. In each pair, the *Osteoborus* bone is on the left.

In modern dogs the entepicondylar foramen is absent. It is curious that *Borophagus*, the terminal member of the hyaenoid dog phylum, also lacks the foramen. So far as known, it is present in earlier hyaenoid dogs.

The radius is shorter than that of the wolf, but stouter. The

shaft is triangular in cross section, rather than flat. The distal end is rotated or twisted until the long axis of the scapholunar articulation is at a 45° angle from the long axis of the articular facet for the humerus. In the wolf, the two are almost parallel. This twisting of the shaft is the same in another, slightly smaller, specimen from the Blanco (MU8036). The radius of *Osteoborus* resembles that of *Borophagus* in shape but is smaller and also has the articular surfaces of the two ends parallel.

The ulna of the skeleton lacks the proximal end but this is present in another specimen (MU8035), which lacks only the distal end. The ulna of *Borophagus* was shorter than that of the wolf, but thicker. The articular facet for the proximal end of the radius is divided by a deep groove. No such groove is present in the wolf. The groove is present in the ulna of *Osteoborus*. The ulna of *Osteoborus* is nearly as large as that of *Borophagus,* and astonishingly similar in shape.

The pisiform is smaller than that of the gray wolf, but generally similar in shape. The unciform facet is relatively small and narrow. The magnum is also similar to but smaller than that of the wolf. The pisiform surface is narrower and the metacarpal surface is less curved. The unciform is longer and narrower than the unciform of the wolf. It has a rectangular rather than triangular metacarpal articular surface. There is considerable individual variation in the size and shape of the articular facets of the carpal elements in *Canis,* and same was probably true of *Borophagus.* Of the known carpals of *Borophagus diversidens,* only the unciform seems to be unique in shape.

The only complete metacarpal available is MC2. It is little more than half the length of the MC2 of the gray wolf. The shaft is rounder, less flattened.

The pelvis is greatly broken and no meaningful measurements can be taken. The bone is shorter and broader than that of the gray wolf. The blade of the ilium is wider and rounder. No pelvis of *Osteoborus* is available for comparison.

The femur lacks the distal end but it is apparent that it was about as long as that of the wolf. The lesser trochanter is very prominent and located lower on the shaft than in the wolf. It is joined to the head of the femur by a distinct ridge, absent in the wolf. The shaft is straight, and in anteroposterior view the head is

set more laterally than that of the wolf. The femur of *Osteoborus* is closely similar to but smaller than that of *Borophagus*.

The tibia is much shorter than that of the wolf, and both proximal and distal ends are smaller. The shaft, however, is relatively thick and is almost *triangular* in cross section. The tibia of *Osteoborus* is smaller than that of *Borophagus* but otherwise almost identical.

The only available *Borophagus* fibula lacks part of the shaft, and its length cannot be determined. The parts on hand are essentially like those of the wolf.

The astragalus is smaller than that of the wolf. The neck is shorter. The navicular surface is almost parallel with the transverse axis of the astragalus rather than rotated 45°, as in the wolf. The calcaneum is strikingly short and broad, as compared with that of the wolf. It is relatively short and broad as compared with that of *Osteoborus* as well. However, the astragalus of *Osteoborus* is almost as large as that of *Borophagus* and differs only in having a less round navicular surface.

The navicular of *Borophagus* is smaller and much flatter than in the wolf, with the calcaneal surface markedly shallow. The cuboid is smaller, anteroposteriorly and dorsoventrally, with the calcaneal surface much compressed anteroposteriorly. The fourth metatarsal (two specimens) are as thick and stout as those of the wolf, but only a bit more than half as long. MT5 is also short and stout, but only about half as long as in the wolf. The metatarsals of *Osteoborus* are not so greatly shortened as in *Borophagus*.

Appendix

Measurements, in millimeters, of the skull are as follows: condylobasal length 212; zygomatic breadth 173; interorbital breadth 50; postorbital breadth 46; breadth across mastoid process 77.5; breadth across occipital condyles 41.5; breadth across incisor row 43.3; breadth across canines 63.6; breadth across first molars 90.2; breadth across second molars 73.5; length I^1 to M^2 103.8; length I^3 to M^1 98.7; length C to P^4 69.2; length C to M^1 83.4; length C to M^2 85.9; length P^4 to M^1 43.4; length P^4 to M^2 49.5.

The upper teeth have the following measurements: I^1 7.5 × 5.7; I^2 7.3 × 7.3; I^3 11.1 × 10.0; C 14.9 × 11.1; P^1 7.6 × 6.7; P^2 10.0 × 7.1; P^3 11.3 × 7.0; P^4 28.7 × 16.1; M^1 17.5 × 23.1; M^2 12.6 × 9.3 mm.

Measurements of the mandible are, length condyle to tip of mandible 170.0; length condyle to anterior face of I_3 168.3; length condyle to anterior face of

canine 160.6; thickness of mandible under P_4 20.1; thickness of mandible under M_1 17.9; height angular process to tip of coronoid process 95.4; length I_3 to M_3 107.3; length C to M_1 85.2; length C to M_3 101.7; length P_4 to M_1 50.5 mm.

The lower teeth have the following measurements: I_3 7.2 × 7.9; C 15.2 × 13.3; P_2 alveolus 6.1 × 4.6; P_3 8.0 × 6.2; P_4 20.0 × 14.3; M_1 32.8 × 14.3; M_2 11.6 × 8.3; M_3 8.3 × 6.4 mm.

Pisiform: greatest length 19.3; greatest height of articular facet for scapholunar 9.9; greatest height of anterior end 12.7 mm.

Magnum: dorsopalmar height 18.5; greatest transverse breadth 10.7; greatest anteroposterior length from center of metacarpal facet 10.5 mm.

Unciform: greatest length of upper (outer) surface 15.0; greatest height measured normal to upper surface 16.4; greatest transverse breadth 12.4 mm.

Metacarpal 2 (right): greatest length 52.5; height, proximal 12.7; transverse breadth, proximal ?; height, midshaft 7.5; transverse breadth, midshaft 7.4; height, distal 10.4; transverse breadth, distal 11.3 mm.

Femur: transverse breadth, head to outer edge of external tuberosity 56.1; vertical diameter of head 22.7; transverse diameter of head 24.6; least anteroposterior constriction of neck 14.5; anteroposterior diameter at midshaft 16.1; transverse diameter at midshaft 18.4 mm.

Tibia: greatest length 182.0; greatest transverse breadth of proximal end 45.2; greatest anteroposterior breadth of proximal end 46.1; transverse breadth at midshaft 14.9; anteroposterior diameter at midshaft 16.5; greatest transverse diameter at distal end 28.9; greatest anteroposterior breadth of distal end 19.9 mm.

Fibula: anteroposterior diameter of proximal end 15.7; transverse diameter of proximal end 8.4; anteroposterior diameter of distal end 14.9; transverse diameter of distal end 8.3 mm.

Astragalus: greatest breadth across tibial surface 17.7; greatest length of outer tibial surface, measured normal to posterior edge 22.8; least vertical height, measured transversely, tibial to calcaneal surfaces 14.6 mm.

Axis: length from anterior end of odontoid process to ventral tip of posterior epiphysis of centrum 54.0; greatest breadth across articular facets for atlas 40.0; greatest breadth across posterior epiphysis of centrum 23.1; greatest breadth across posterior zygapophyses 44.9; height from central lip of posterior epiphysis of centrum to top of neural spine 59.3 mm.

Seventh cervical vertebra: length of centrum measured normal to posterior face 21.4; breadth of anterior epiphysis of centrum 20.5; breadth across anterior zygapophyses 42.3; breadth across posterior zygapophysis 41.3; length from anterior to posterior zygapophysis 34.8; height from ventral lip of posterior epiphysis of centrum to top of neural spine 71.4 mm.

Humerus: greatest length 214.4; greatest anteroposterior diameter of proximal end 55.8; transverse diameter at midshaft 18.7; greatest transverse diameter at distal end 58.7; least anteroposterior diameter of distal end anterior to ulnar fossa 16.7 mm.

Radius: greatest length 185.0; greatest transverse diameter at proximal end 24.2; greatest anteroposterior diameter at proximal end 16.6; transverse diameter at midshaft 14.6; anteroposterior diameter at midshaft 14.9; greatest transverse diameter at distal end 32.5; greatest anteroposterior diameter at distal end 23.1 mm.

Ulna (composite of two): greatest length, approximately 120.0; anteroposterior length of olecranon at top of humeral notch 38.0; greatest transverse thickness of back of olecranon 19.8; greatest breadth of articulate surface for radius 19.9; anteroposterior diameter of distal end 16.6 mm.

Calcaneum: greatest length 50.2; least transverse breadth posterior to astragalar surface 10.1; least vertical height posterior to astragalar surface 17.5; breadth across anterior astragalar surfaces 21.6 mm.

Navicular: greatest transverse diameter 20.0; greatest anteroposterior diameter 15.8; greatest height of anterior (outer) surface 9.4 mm.

Cuboid: height, calcaneal to cuneform surfaces 17.9; greatest anteroposterior length 14.2; greatest transverse breadth 14.8 mm.

Metatarsal 4 (mean measurements of two): greatest length 62.1; height, proximal 14.4; transverse breadth, proximal 11.4; height, midshaft 7.5; transverse breadth, proximal 8.8; height, distal 11.0; transverse breadth, distal 12.4 mm.

Metatarsal 5 (right): greatest length 58.3; height, proximal 14.1; transverse breadth, proximal 12.8; height, midshaft 7.9; transverse breadth, midshaft 6.8; height, distal 10.0; transverse breadth, distal 10.2 mm.

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